

females examined in the following species. These species are arranged in seven groups that would be separated at a generic level in a conservative taxonomic treatment.

Tribolonotus. This highly distinctive genus of spiny skinks occurs in New Guinea, the Admiralty Islands, the Bismarck Archipelago and the Solomon Islands (Zweifel, 1966; Greer and Parker, 1968a; and Cogger, 1972). The species are cryptic and are generally found only under surface cover such as rocks, logs and piles of litter. Current work indicates that *Tribolonotus* may be part of the same radiation that gave rise to the Australian Region's well known skink taxa *Corucia*, *Egernia*, and *Tiliqua* (Greer, personal observation), all of which apparently have paired oviducts.

The reproductive tracts of four of the eight species of *Tribolonotus* have been examined (*blanchardi*, *gracilis*, *pseudoponceleti* and *schmidti*) and in all the left oviduct was either absent or vestigial. Due to the fact that these species represent much of the ecological, morphological and geographical diversity in the genus (see references cited above), it is reasonable to assume that the genus as a whole lacks the left oviduct. The mode of reproduction is known for all four species mentioned above: the first three are oviparous; *T. schmidti* is viviparous.

Sphenomorphus aignanus, *S. bignelli*, *S. louisiadensis* and *S. minutus*. Despite the fact that these four species of the Papuan-Solomon Islands area are currently placed in the genus *Sphenomorphus*, they bear only a superficial resemblance to the various other groups that make up this extremely diverse assemblage. Phylogenetically they are probably members of the radiation that gave rise to a large number of other well known taxa of the Australian Region such as *Eugongylus*, *Leiolopisma* and *Emoia* (Group II of Greer, 1974), all of which apparently have paired oviducts.

These four species fall into two distinct subgroups on the basis of size and ecology. *Sphenomorphus aignanus* of eastern New Guinea, the D'Entrecasteaux Archipelago and the Louisiade Archipelago, and *S. louisiadensis* of the Louisiade Archipelago, are medium sized skinks which are probably surface dwelling forms judging from their size and limb proportions, whereas *S. minutus* of New Guinea and *S. bignelli* of the Solomon Islands are relatively small and are known to be cryptic inhabitants of the litter (Fred Parker, personal communication). These differences raise the possibility that these two subgroups lost the left oviduct independently of each other. All four species are oviparous.

Geomyersia glabra. This small, depressed skink is endemic to the northern Solomon Islands where it inhabits surface litter. The genus is monotypic and appears to have been derived from a small group of east Australian skinks (*Lampropholis*; Greer and Parker, 1968b; and Greer, 1974) all of which have paired oviducts. *Geomyersia glabra* is oviparous.

Lipinia leptosoma. This small arboreal species is endemic to the Palau Islands where to date it has only been found in the crowns of screw pine *Pandanus* (Brown and Fehlmann, 1958). The species' congeners are centered over the Philippines and New Guinea (Greer, 1974) and, as far as is known, all have paired oviducts. *L. leptosoma* is viviparous.

Sphenomorphus schultzei. This is a small New Guinea member of the *fasciatus* species group of *Sphenomorphus*—a group that has radiated extensively throughout northern Australia, New Guinea, the Bismarck Archipelago and the Solomon Islands (Greer and Parker, 1967 and 1974). *S. schultzei* inhabits dense rain forest in deep valleys where it lives under decaying logs and vegetable matter on the forest floor. As far as is known all other members of the species group have paired oviducts. *S. schultzei* is oviparous.

Sphenomorphus steerei. This is a small Philippines endemic whose closest relatives appear to be the other small "*Sphenomorphus*" of the Archipelago (personal observation). *S. steerei* is a relatively common species in the forest where it is found by day both on the surface and beneath surface objects such as rocks, logs and debris (Brown and Alcalá, 1961). The close relatives of this species which have been examined have paired oviducts. *S. steerei* is oviparous.

Sphenomorphus consobrinus. This species occurs in the northern Moluccas. Its exact relationships within the vast polyphyletic *Sphenomorphus* assemblage are uncertain. It could be part of the radiation that gave rise to the small "*Sphenomorphus*" of the Philippines and the western end of the Indo-Australian Archipelago, or it could be related to the *fasciatus* species group of *Sphenomorphus* (personal observation). The species does not, however, appear to be related closely enough to either *steerei* among the small Philippine "*Sphenomorphus*" or to *schultzei* of the *fasciatus* species group to have the loss of its oviduct ascribed to close relationship with either of these two taxa. Nothing is known of this species' ecology. It is probably oviparous judging from the texture of the shell surrounding the egg in the one gravid female I examined.

There are three important facts associated with the loss of an oviduct in these skinks. Firstly, anatomical observations reveal that whenever an oviduct has been lost in skinks, it has invariably been the left oviduct and never the right. Secondly, my own phylogenetic studies (references cited above and work in progress) make it fairly clear that this oviduct has been lost at least seven and perhaps eight different times in scincid lizard evolution. And thirdly, a fact that has not been alluded to before but which is nevertheless crucial, is that the skinks which lack the left oviduct are, with only one, or possibly two exceptions, unique among skinks in having a constant brood size of one (personal observation, Table 1).¹ The limbless African burrower *Typhlosaurus garipeensis* is the only well known exception. This species has a brood size of one (N=11; Huey *et al.*, 1974) and appears to have paired oviducts. The only specimens available to me for gross examination had the oviducts in a very regressed state. Another limbless burrower, *Isopachys roulei* of southeast Asia, may also have a litter size of one, although the information available on this point (Taylor, 1963) is ambiguous; it too has paired oviducts (personal observation). All other skinks examined to date (N=300+species), including many of the closest relatives of the skinks with one oviduct, have brood sizes averaging more than one, and they have paired oviducts.

DISCUSSION

The reptiles now known to have lost the left oviduct can be divided into two distinct groups on the basis of external morphology, adaptive mode, brood size and distribution. The first group includes the lizard genus *Anniella* and all the snake genera. Members of this group are relatively narrow bodied, attenuate, limbless squamates which are largely restricted to a burrowing habit. Furthermore, they all apparently have variable brood sizes (except for *Tantilla planiceps* which has a brood size of one—Stebbins, 1954; Minton, 1959; and personal observation), and they are distributed in both temperate and tropical areas.

The second group includes the scincid lizards largely described here for the first time. In contrast to the first group, members of this group are fully limbed, pentadactyl squamates which occur in a variety of adaptive zones ranging from

¹ Two species of *Tribolonotus* that are known to have a brood size of one have not been examined for the presence or absence of the left oviduct (*annectens*, N=2 and *novaeguineae*, N=1). It would, however, be remarkable if either of these species retained the oviduct given the fact that the other species of *Tribolonotus* which are known to have lost the oviduct are broadly representative of the genus in terms of morphology, ecology and distribution.

TABLE 1

Reproductive data for the scincid lizards which have lost the left oviduct. The species are arranged in their most conservative generic level taxa. Sample sizes are given in parenthesis

Taxon	Number of specimens examined for the loss of an oviduct	Number of specimens examined for brood size	Minimum snout-vent length of ♀♀ at maturity (mm)	Frequency of individuals with an oviducal egg or young having, in addition, a yolky egg in either ovary	Frequency of individuals with a yolky ovarian egg having the egg in the left ovary
(1) <i>Tribolonotus blanchardi</i>	13	13	31 (9)	0.00 (3)	0.14 (7)
<i>schmidti</i>	12	12	33 (12)	0.10 (10)	1.00 (1)
<i>pseudoponceleti</i>	58	102	44 (102)	0.21 (38)	0.36 (28)
<i>gracilis</i>	1	4	87 (4)	— (0)	— (0)
(2) " <i>Sphenomorphus</i> "	19	22	31 (21)	— (0)	0.33 (6)
<i>bignelli</i>	1	2	37 (1)	— (0)	0.00 (1)
<i>minutus</i>	2	2	44 (2)	0.00 (1)	0.00 (1)
<i>louisianensis</i>	2	5	61 (5)	0.66 (3)	0.33 (3)
<i>aiguanus</i>	5	5	61 (5)	0.66 (3)	0.33 (3)
(3) <i>Geomyersia glabra</i>	2	2	31 (2)	0.00 (1)	— (0)
(4) <i>Lipinia leptosoma</i>	7	7	37 (7)	0.00 (3)	1.00 (1)
(5) " <i>Sphenomorphus</i> "	4	4	35 (3)	0.00 (2)	— (0)
<i>fasciatus</i> species group schultzei "	13	24	27 (20)	0.50 (6)	0.44 (9)
(6) " <i>Sphenomorphus</i> "	1	1	38 (1)	1.00 (1)	1.00 (1)
<i>steerei</i>					
(7) " <i>Sphenomorphus</i> "					
<i>consobrinus</i>					

subfossorial to arboreal (see above). All of the members of the group have a constant brood size of one and all occur only on islands in the tropics.

The reasons for the loss of the left oviduct appear to have been different in each of these two groups. Other writers have suggested that the oviduct has been lost in the first group due to the difficulties that a relatively long but narrow bodied form might have in accommodating two parallel oviducts full of eggs in the confines of a subterranean habitat (Fox and Dessauer, 1962; Clark, 1970a). According to this hypothesis it is thought that the increased girth caused by pregnancy would increase the frictional forces encountered in burrowing and would also limit the number and kind of underground pathways available for foraging and escape. This is a reasonable first order hypothesis but it should be borne in mind that the reproductive tracts of many burrowing squamates, especially snakes, have not been examined and that there are many burrowing forms that are definitely known to retain paired oviducts; for example, all amphisbaenians (C. Gans, personal communication) the extremely thin pygopodid *Apraxis striolata* (personal observation), many skinks (personal observation), and the following snakes: *Carphophis* (Clark, 1970b), *Cylindrophis rufus* (Bergman, 1953), *Liotyphlops* (Robb and Smith, 1966), several species of *Tantilla* (Clark, 1970a) and all uropeltids (C. Gans, personal communication). These "exceptional" forms indicate that common above ground methods of filling two oviducts are employed by some burrowers (perhaps due to subtle differences in their ecologies) or, additionally, that there are novel solutions to the packing problem in certain burrowers that have yet to be investigated.

What I believe to be a sound general explanation for the loss of the oviduct in the second group, that is, the skinks, is based on the group's exclusively tropical distribution and unusually low brood size of one, and it is most readily understood as a variation of a reproductive strategy that seems to be characteristic of many tropical lizards. The available evidence for skinks indicates that, as in other lizard species (Tinkle *et al.*, 1970), tropical species seem to mature earlier than temperate species,² and, if they are like other lizards (Tinkle *et al.*, 1970) tropical skink species probably also produce more broods per season than temperate species.³ In other words, the general reproductive strategy in many tropical skinks may be geared to early and repeated reproduction. In this context, species with a brood size of one might become even more reproductively efficient if the energy required for the development and maintenance of the "extra" oviduct were reallocated through selection to other functions.

One problem with this efficiency hypothesis, however, is that it does not seem to apply to other tropical lizards that apparently have a constant brood size of one: the anolines (Smith *et al.*, 1973) among the iguanids; *Aristelliger* (Hecht, 1952), *Gehyra variegata* (Bustard, 1968) and the sphaerodactylines (Kluge, 1967) among the gekkonids; *Gonocephalus nigrigularis* (personal observation) among the agamids; *Proctoporus guntheri* (Uzzell, 1970), *Ecleopopus quadrichaudii* (Uzzell, 1969), *Bachia monodactylus* (Dixon, 1973) among the teiids, and *Chirindia ewerbecki* (Loveridge, 1941) among the amphisbaenians. In contrast to skinks, all of these taxa in which the oviducal anatomy has been examined (the first six

² Data on age at maturity exist for 20 of the 800+ species of skinks (personal observation). If an age of twelve months is arbitrarily taken as the dividing point between early and late maturity (this follows Tinkle *et al.*, 1970), then early maturity is significantly more characteristic of tropical than temperate species ($P = .02$, Fisher Exact Probability Test).

³ This supposition is supported but not proved for skinks that lack the left oviduct, all of which are tropical, by the fact that where the sample sizes are large enough to provide a fair indication, the females of these species often have both an oviducal egg or embryo and a yolking ovarian egg (Table 1). This suggests at least the potentiality for a quick second brood.

taxa listed) have paired oviducts (personal observation). The difference between the skinks and these other lizard taxa is highlighted by considering the number of times brood size was reduced to one in each of the two groups and the fate of the oviduct with each reduction. In each of the nonscincid taxa listed above, the evolution of a constant brood size of one can be reasonably interpreted as an independent event, and in none of the six taxa in which the oviducal anatomy has been examined has the reduction in brood size been accompanied by the loss of an oviduct. In the tropical skinks, on the other hand, a constant brood size of one has evolved independently at least seven, and perhaps eight times (depending on whether group 2 above is mono or diphyletic with regard to the evolution of brood size), and in each case the reduction was accompanied by the loss of the left oviduct. This indicates that in tropical skinks the loss of the left oviduct is closely correlated with a reduction in brood size to one. The only possible exception to this generalization is the Southeast Asian *Isopachys roulei* which, as discussed above, may have a brood size of one but definitely has paired oviducts.

There is no obvious explanation for this difference between these two groups of lizards. A hypothesis that is appealing due to its generality, but difficult to test, is that skinks are under greater duress to conserve the energy that would otherwise go into development and maintenance of an oviduct than are the other lizards, perhaps because they are in more competitive or predator-ridden habitats (see below).

It is interesting to compare the reproductive aspects of the life history that has been inferred above for those skinks which have a brood size of one and only one oviduct, with the well known life history of *Typhlosaurus garipeensis* which has a brood size of one (Huey *et al.*, 1974) but retains both oviducts (personal observation). The most significant difference between these two groups, as it relates to the hypothesis that the skinks with one oviduct have found it selectively advantageous to rechannel the energy required to develop and maintain the second oviduct into other functions, is that *T. garipeensis*, like other temperate lizards, has a relatively lengthy age to maturity (one and two-thirds year) and reproduces infrequently (one brood per year, (Huey *et al.*, 1974)) whereas the other skinks, like other tropical lizards, are inferred to have a relatively short age to maturity and to reproduce frequently. Given this relatively longer age to maturity and lower reproductive rate, the energy *T. garipeensis* might save by eliminating the second oviduct may not be enough to offset the benefit of retaining the oviduct for some long term use, for example, in producing two young per brood in an exceptionally "favourable" year or at an older age.

It remains to be seen whether the tropical Southeast Asian limbless, burrowing skink *Isopachys roulei* has a brood size of one. However, if it does, it would be exceptional among tropical skinks with a similar brood size in retaining paired oviducts.

Although a reduction in brood size to one appears to be a key factor in the loss of an oviduct in skinks, one might reasonably wish to ask why brood size has been reduced to one in these species. This problem is related in part to the general trend, observed in other lizards as well as in skinks, for tropical species to have smaller brood sizes than temperate species.⁴ Although the reasons for this trend are not obvious, two hypotheses have recently been suggested. Tinkle *et al.* (1970) have suggested that tropical species live in a highly competitive environment and may have increased egg size at the expense of brood size thereby

⁴ For skinks this statement is based on a comparison of the overall average brood size of 70 tropical species ($\bar{X}=2.69$, $s^2=2.16$) and 22 temperate species ($\bar{X}=4.79$, $s^2=5.41$), each species being represented by an average brood size derived from a sample of five or more broods ($t'=3.99$, $P<.001$; Snedecor and Cochran, 1967: 114-116; Greer, unpublished data).

increasing the size and hence the competitiveness of the young. Andrews and Rand (1974), however, think that tropical species are more stressed by predation than competition and have emphasized brood frequency at the expense of brood size thereby maximizing their reproductive contribution prior to their almost certain early death, the presumption being that the shorter life expectancy makes it too risky to spend a great deal of time yolking a large brood. It is debatable which of these two hypotheses is nearer to the truth for the tropical skinks with only one oviduct, but the operative factor in either hypothesis, that is, increased competition or increased predation, could provide the ultimate selective force for reallocating the energy that would otherwise go into the development and maintenance of one of the two oviducts in these skinks.

Finally, as pointed out above, in each of the seven or eight skink lineages in which the oviduct has been lost independently, it has always been the left oviduct which has been lost and not the right. This is also true of all the other squamate lines which have lost an oviduct. The reason for this seems fairly clear. In most squamates the left member of normally paired organs, such as lungs and oviducts, is generally smaller than the right member—perhaps due to the fact that other unpaired organs, such as the stomach, lie on the left side—and hence the loss of this smaller member is presumably proportionately less disruptive to developmental processes. Amphisbaenians are an exception to this generalization due to the fact that they have reduced or lost the right lung instead of the left (Butler, 1895).

It is significant, however, that as far as is known, all of the skinks that have lost the left oviduct have retained a functional left ovary (Table 1), and as far as is known this is also true of the other squamate lines that have lost the oviduct. This indicates that, although selection has presumably mediated the loss of one of the two bilateral conduits for transporting the eggs and young to the outside world, it has left intact the bilateral machinery for producing the eggs. It is interesting to note that prior to ovulation the left ovary generally shifts over to the right side in skinks (personal observation).

ACKNOWLEDGEMENTS

Most of the material that I have examined during the course of this study is in the Museum of Comparative Zoology at Harvard College under the curatorial care of Professor Ernest Williams. Needless to say Professor Williams' generosity and encouragement have been vital to this work. Two other curators have also been helpful in supplying crucial material, namely, Dr. W. D. Haacke of the Transvaal Museum for supplying female *Typhlosaurus garipeensis* and Mr. Hymen Marx of the Field Museum for providing female *Isopachys roulei*. I have also benefited greatly from Professor Carl Gans' generous summaries of amphisbaenian and uropeltid anatomy. Finally, the following readers have aided me substantially by providing criticisms of various drafts of this paper: Dr. Harold Cogger, Ms. Bonnie Dalzell, Dr. Raymond Huey, Ms. Phylp Greer, Dr. Lynette Moffat, and Mr. Peter Rankin.

References

- ANDREWS, R. and RAND, A. S., 1974.—Reproductive effort in anoline lizards. *Ecology*, 55 : 1317–1327.
- BERGMAN, R. A. M., 1953.—The anatomy of *Cylindrophis rufus*. *Proc. K. Ned. Akad. Wet. Amsterdam, Ser. C.*, 56 (5) : 650–712.
- BROWN, W. C. and ALCALA, A. C., 1961.—Populations of amphibians and reptiles in the submontane and montane forests of Cuernos de Negros, Philippine Islands. *Ecology* 42 (4) : 628–636.
- BROWN, W. C. and FEHLMANN, A., 1958.—A new genus and species of arboreal scincid lizards from the Palau Islands. *Occ. Pap. Nat. Hist. Mus. Stanford Univ.*, No. 6, 7 pp.
- BUSTARD, H. R., 1968.—The reptiles of Merriwindi State Forest, Pilliga West, northern New South Wales, Australia. *Herpetologica* 24 (2) : 131–140.

- BUTLER, G. W., 1895.—On the complete or partial suppression of the right lung in the Amphisbaenidae or of the left lung in snakes and snake-like lizards and amphibians. *Proc. Zool. Soc. London*, 1895 : 691-712.
- CLARK, D. R. JR., 1970a.—Loss of the left oviduct in the colubrid snake genus *Tantilla*. *Herpetologica* 26 (1) : 130-133.
- , 1970b.—Ecological study of the Worm Snake *Carphophis vermis* (Kennicott). *Univ. Kans. Publ. Mus. Nat. Hist.* 19 (2) : 85-194.
- COE, W. R. and KUNKEL, B. W., 1906.—Studies on the California limbless lizard, *Anniella*. *Trans. Conn. Acad.* 12 (1) : 1-55.
- COGGER, H. G., 1972.—A new scincid lizard of the genus *Tribolonotus* from Manus Island, New Guinea. *Zool. Meded. Rijks Mus. Nat. Hist. Leiden*, 47 : 202-210.
- DIXON, J. R., 1973.—A systematic review of the teiid lizards, genus *Bachia*, with remarks on *Hcterodactylus* and *Anotosaura*. *Univ. Kan. Mus. Nat. Hist. Misc. Publ.*, No. 57, 47 pp.
- FOX, W. and DESSAUER, H. C., 1962.—The single right oviduct and other urogenital structures of female *Typhlops* and *Leptotyphlops*. *Copeia* 1962 (3) : 590-597.
- GREER, A. E., 1974.—The generic relationships of the scincid lizard genus *Leiolopisma* and its relatives. *Aust. J. Zool.*, Suppl. Ser., No. 31, 67 pp.
- and PARKER, F., 1967.—A new scincid lizard from the northern Solomon Islands. *Breviora* No. 275, 20 pp.
- , 1968a.—A new species of *Tribolonotus* (Lacertilia : Scincidae) from Bougainville and Buka, Solomon Islands, with comments on the biology of the genus. *Breviora* No. 291, 23 pp.
- , 1968b.—*Geomyersia glabra*, a new genus and species of scincid lizard from Bougainville, Solomon Islands, with comments on the relationships of some lygosomine genera. *Breviora* No. 302, 17 pp.
- , 1974.—The *fasciatus* species group of *Sphenomorphus* (Lacertilia : Scincidae) : notes on eight previously described species and descriptions of three new species. *Papua New Guinea Sci. Soc. Proc.*, 25 : 31-61.
- HECHT, M. K., 1952.—Natural selection in the lizard genus *Aristelliger*. *Evolution*, 6 : 112-124.
- HUEY, R., PIANKA, E. R., EGAN, M. E. and COONS, L. W., 1974.—Ecological shifts in sympatry : Kalahari fossorial lizards (*Typhlosaurus*). *Ecology* 55 (2) : 304-316.
- KLUGE, A. G., 1967.—Higher taxonomic categories of gekkonid lizards and their evolution. *Bull. Am. Mus. Nat. Hist.* 135 (1) : 1-60.
- LOVERIDGE, A., 1941.—Revision of the African lizards of the family Amphisbaenidae. *Bull. Mus. Comp. Zool.*, 87 (5) : 353-451.
- MINTON, S. A. JR., 1959.—Observations on amphibians and reptiles of the Big Bend region of Texas. *Southwest. Nat.*, 3 : 28-54.
- ROBB, J. and SMITH, H. M., 1966.—The systematic position of the group of snake genera allied to *Anomalopis*. *Nat. Hist. Misc.*, No. 184, 8 pp.
- SMITH, H. M., SINELENIK, G., FAWCETT, J. D., and JONES, R. E., 1973.—A survey of the chronology of ovulation in suoline lizard genera. *Trans. Kans. Acad. Sci.*, 75 (2) : 107-120.
- SNEDECOR, G. W., and COCHRAN, W. G., 1967.—*Statistical Methods*. Iowa State Univ. Press, Ames, Iowa ; 593 pp.
- STEBBINS, R. C., 1954.—*Amphibians and Reptiles of Western North America*. McGraw-Hill Book Co., Inc., New York ; 528 pp.
- TAYLOR, E. H., 1963.—The lizards of Thailand. *Univ. Kans. Sci. Bull.*, 44 (14) : 687-1077.
- TINKLE, D. W., WILBUR, H. M., and TILLEY, S. G., 1970.—Evolutionary strategies in lizard reproduction. *Evolution*, 24 (1) : 55-74.
- UZZELL, T., 1969.—The status of the genera *Ecleopopus*, *Arthroseps* and *Aspidolaemus* (Sauria, Teiidae). *Postilla*, No. 135, 23 pp.
- , 1970.—Teiid lizards of the genus *Proctoporus* from Bolivia and Peru. *Postilla*, No. 142, 39 pp.
- ZWEIFEL, R. G., 1966.—A new lizard of the genus *Tribolonotus* (Scincidae) from New Britain. *Am. Mus. Novit.*, No. 2264, 12 pp.

FOUR-WINGED DIPTERA FROM THE UPPER PERMIAN OF AUSTRALIA

E. F. RIEK*

(Plate XI)

[Accepted for publication 21st July 1976]

Synopsis

A complete specimen of *Choristotanyderus nanus* Riek shows that the species had four wings and that the hind wing was about two-thirds as long as the fore wing. The fore wing has the characteristic kink in the stem of R that is diagnostic of the Diptera. The species differs from Mecoptera, also, in having R straight at the origin of Rs in the fore wing. The species retains the plesiomorphic characters of a large pterostigma, 4-branched Rs and M, distinct CuP widely separated from CuA, and at least two long anal veins and very probably a distinct third anal. The fore wing is similar to that of *Permotanyderus*, which very probably had a hind wing as large as the fore wing. The family Permotanyderidae, embracing only *Permotanyderus* and *Choristotanyderus*, is referred to the Diptera and placed in a new suborder Perrisoptera. The suborder cannot be defined phylogenetically but is used for convenience to accommodate Diptera with four wings.

INTRODUCTION

Riek (1953) described the fore wing (considered doubtfully as a hind wing) of *Choristotanyderus nanus* and placed the species in the Permotanyderidae because, although the basal stem of R with the kink diagnostic of the Diptera had not been preserved, as it is in *Permotanyderus ableptus* Riek (1953), the origin of Rs from R was similar to that in *Permotanyderus* and differed from that typical of Mecoptera, in which the stem of R is distinctly curved (concave) at the origin of Rs. The stem of R is straight at the origin of Rs in *Permotanyderus* and *Choristotanyderus*, as in Diptera. Riek placed the Permotanyderidae in Mecoptera, suborder Protodiptera because it seemed probable that the species had four wings. He restricted the order Diptera to species known to have only two wings.

The limits and affinities of the Protodiptera have varied. Crampton included the Paratrachoptera in the Protodiptera whereas Martynova (1962), while adopting much the same limits for the group, used the term Paratrachoptera. Tillyard (1937) distinguished between these two orders and relegated them to suborder status within an enlarged order Mecoptera. Riek (1953) adopted the classification proposed by Tillyard. Tillyard (1937) figured, but did not name, a species from the Upper Permian of Belmont (including the Warner's Bay area), Australia, that he referred to the Protodiptera because it had four wings, each of which was said to resemble those of Diptera. The species was subsequently named *Robinjohnia tillyardi* by Martynova (1948), and referred to a separate family that she considered ancestral to Neorthophlebiidae (Eumecoptera). Later (1961) she synonymised the Robinjohniidae with the Permotipulidae and (1962) referred the Permotipulidae to the Paratrachoptera (including Protodiptera). Tillyard (1929) described *Permotipula patricia* from a single wing, also from the Upper Permian of Belmont, and placed the family Permotipulidae in the superfamily Tipuloidea (Diptera), because of similarity in venation to that of Recent Tipulidae, from which it differed in the slight degree of petiolation, the short 2A and the elongate median cell. The affinities of the species remain obscure since the type is lost. It cannot be referred to the Diptera because it does not have the

* CSIRO Division of Entomology, P.O. Box 1700, Canberra City, ACT, 2601.